J Arid Land (2023) 15(11): 1405–1420
https://doi.org/10.1007/s40333-023-0071-y

Science Press Springer-Verlag

Plant growth-promoting properties and anti-fungal activity of endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* in arid lands

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Abstract: Endophytes, as crucial components of plant microbial communities, significantly contribute to enhancing the absorption of nutrients such as nitrogen and phosphorus by their hosts, promote plant growth, and degrade pathogenic fungal mycelia. In this study, an experiment was conducted in August 2022 to explore the growth-promoting potential of endophytic bacterial strains isolated from two medical plant species, *Thymus altaicus* and *Salvia deserta*, using a series of screening media. Plant samples of *Thymus altaicus* and *Salvia deserta* were collected from Zhaosu County and Habahe County in Xinjiang Uygur Autonomous Region, China, in July 2021. Additionally, the inhibitory effects of endophytic bacterial strains on the four pathogenic fungi (*Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*) were determined through the plate confrontation method. A total of 80 endophytic bacterial strains were isolated from *Thymus altaicus*, while a total of 60 endophytic bacterial strains were isolated from *Salvia deserta*. The endophytic bacterial strains from both *Thymus altaicus* and *Salvia deserta* exhibited plant growth-promoting properties. Specifically, the strains of *Bacillus* sp. TR002, *Bacillus* sp. TR005, *Microbacterium* sp. TSB5, and *Rhodococcus* sp. TR013 demonstrated strong cellulase-producing activity, siderophore-producing activity, phosphate solubilization activity, and nitrogen-fixing activity, respectively. Out of 140 endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta*, 104 strains displayed anti-fungal activity against *Fulvia fulva*, *Alternaria solani*, *Fusarium oxysporum*, and *Valsa mali*. Furthermore, the strains of *Bacillus* sp. TR005, *Bacillus* sp. TS003, and *Bacillus* sp. TSB7 exhibited robust inhibition rates against all the four pathogenic fungi. In conclusion, the endophytic bacterial strains from *Thymus altaicus* and *Salvia deserta* possess both plant growth-promoting and anti-fungal properties, making them promising candidates for future development as growth-promoting agents and biocontrol tools for plant diseases.

Keywords: endophytic bacteria; *Thymus altaicus*; *Salvia deserta*; pathogenic fungi; plant growth-promoting properties; anti-fungal activity

Citation: ZHAO Mengqi, SU Huan, HUANG Yin, Rashidin ABDUGHENI, MA Jinbiao, GAO Jiangtao, GUO Fei, LI Li. 2023. Plant growth-promoting properties and anti-fungal activity of endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* in arid lands. Journal of Arid Land, 15(11): 1405–1420. https://doi.org/10.1007/s40333-023-0071-y

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Received 2023-03-07; revised 2023-08-04; accepted 2023-08-13

1 Introduction

Thymus altaicus, a perennial aromatic plant, is known for its adaptability to harsh habitats such as drought, barrenness, and salinity. It thrives in arid, semi-arid, and barren riverbank and hilly areas, exhibiting strong stress-resistance and adaptability (Prasanth et al., 2014; Patil et al., 2021). As a medicinal plant, *Thymus altaicus* produces a variety of bioactive compounds with antibacterial, antioxidant, anti-aging, and antineoplastic properties (Zarzuelo and Crespo, 2002; Wu et al., 2012; Abaza et al., 2015; Aljabeili et al., 2018; Abdel-Gabbar et al., 2019; Zerroug and Sadrati, 2022). These compounds have wide applications in food, medicine, cosmetics, and other industries (Kumar et al., 2008; Grigore et al., 2010; Sharangi and Guha, 2013).

Salvia deserta, an annual or perennial herb or shrub, predominantly grows in mountainous regions (Wu et al., 2012). It is highly adaptable, thriving in the Tianshan Mountains, with significant diurnal temperature fluctuations, high altitudes, and intense ultraviolet radiation (Sun et al., 2012). *Salvia deserta* produces various compounds, such as steroids, polyphenols, and terpenoids, which exhibit antibacterial, antioxidant, and antineoplastic effects (Zhang and Wang, 2006; Adrar et al., 2016; Rowshan and Najafian, 2020).

Endophytes are microorganisms that reside within healthy plant tissues without causing disease (Schulz and Boyle, 2006). These endophytic microorganisms, isolated from *Thymus* and *Salvia*, exhibit significant potential as biofertilizers and biocontrol agents. Previous studies have demonstrated the growth-promoting effects of endophytic bacterial strains from *Thymus vulgaris* on tomatoes under salt stress and their ability to inhibit *Fusarium oxysporum* pathogenesis (e.g., Abdelshafy Mohamad et al., 2020). Additionally, endophytic bacterial strains isolated from *Salvia* have been shown to promote muskmelon seed growth (Duan et al., 2013) and play a crucial role in plant–bacteria interactions through bioactive alkaloid production (Li et al., 2013).

Endophytes promote plant growth by secreting growth hormones, such as indole-3-acetic acid (IAA), cytokinin (CTK), and gibberellin (GA) (Numan et al., 2018; Wagi and Ahmed, 2019; Palberg et al., 2022). Furthermore, they enhance plant growth by converting nutrients that are unavailable to plants into forms that can be directly absorbed through processes such as nitrogen fixation, phosphate solubilization, and siderophore synthesis (Chaturvedi et al., 2016). Studies have identified that endophytic strains are capable of converting nitrogen into plant-available ammonium or nitrate nitrogen through enzymatic reactions (Hongrittipun et al., 2014) and converting inorganic phosphorus into plant-available phosphate (Lucero et al., 2021). Given the strong adaptability of *Thymus altaicus* and *Salvia deserta* to poor and harsh habitats, endophytic bacterial strains are hypothesized to play a crucial role in their adaptability and stress-resistance.

Endophytes can inhibit the growth and colonization of pathogens by producing metabolites with antimicrobial activity, such as antibiotics, siderophores, chitinases, cellulases, and proteases (Mishra et al., 2020). They can also compete for ecological niches against pathogens (Beneduzi et al., 2012) and produce enzymes that break down pathogen cell walls (Chernin and Chet, 2002). Previous research has shown that endophytes can protect host plants by inhibiting pathogens through the production of specific enzymes (Cardoso et al., 2020). Moreover, endophytes of medicinal plants have been found to produce metabolites with medicinal properties similar or identical to those of their host plants due to their synergetic evolution (Ludwig-Müller, 2015). Consequently, it is hypothesized that endophytes of *Thymus altaicus* and *Salvia deserta* produce substances with antimicrobial activity similar to their host plants, protecting them against pathogens.

Although the biological functions of endophytes from various plant species have been studied, research on the probiotic and anti-phytopathogenic activities of endophytes from *Thymus altaicus* and *Salvia deserta* in arid lands in Xinjiang Uygur Autonomous Region, China, remains limited. This study aims to investigate the plant growth-promoting properties and anti-fungal activity of endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* to offer valuable strain resources and a theoretical basis for enhancing crop quality and yield in agricultural production and controlling plant diseases in arid lands.

2 Materials and methods

2.1 Materials

2.1.1 Collection and pretreatment of plant samples

Focusing on the distribution of *Thymus altaicus* and *Salvia deserta*, our study involved sample collection from Zhaosu County (43°02′N, 80°59′E) and Habahe County (48°29′N, 88°13′E) in Xinjiang Uygur Autonomous Region, China. In July 2021, samples were gathered from locations where both plant species exhibited flourishing growth and development. Prior to sampling, we carefully loosened the surrounding soil to minimize damage to neighboring plants. Entire plants were then excavated and transported to the State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences located in Urumqi City, Xinjiang, using sterile sampling bags, and three samples of each plant were collected, with a total of six samples. Upon arrival, we identified plant samples based on morphological characteristics and surface-sterilized in Vertical superclean bench (SW CJ-2FD, Shanghai Boxun Medical Biological Instrument Corp., Shanghai, China) following established protocols (Li et al., 2018). Endophytic microorganisms were isolated using a combination of serial dilution and plate spreading techniques. The culture plates were incubated at 28°C for 7–14 d, after which all isolated strains were identified by GStorm Gradient PCR (C1000, Bio-RAD, California, the United States), and preserved at ultra cold storage freezer (900 SERIES, Thermo Fisher Scientific, Waltham, the United States) at –80°C for further analysis (Li et al., 2018).

2.1.2 Test strains

A total of 80 endophytic bacterial strains were isolated from *Thymus altaicus*, comprising 15 species from 8 genera, while 60 strains were obtained from *Salvia deserta*, representing 19 species from 9 genera. In total, 140 strains were identified across 4 phyla, 8 orders, 9 families, 12 genera, and 26 species. The isolated strains belonged to the following genera: *Micrococcus*, *Kocuria*, *Dietzia*, *Corynebacterium*, *Microbacterium*, *Rhodococcus*, *Arthrobacter*, *Enterobacter*, *Klebsiella*, *Escherichia*, *Pseudomonas*, and *Bacillus* (Table 1). The endophytic bacterial strains demonstrated significant diversity at both the genus and species levels in different tissues of *Thymus altaicus* and *Salvia deserta* (Figs. 1 and 2).

The tested pathogenic fungi included *Fulvia fulva* and *Alternaria solani*, which are responsible for tomato fusarium wilt (Mandal et al., 2009) and tomato leaf mold (Curtis et al., 1994), respectively. *Fusarium oxysporum* causes cotton fusarium wilt (Halpern et al., 2018), while *Valsa mali* is responsible for apple valsa canker (Ke et al., 2013). These four pathogenic fungi pose significant challenges to agricultural development in arid lands and are preserved at the State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences.

Table 1 Distribution of endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta*

Phylum	Order	Family	Genus	Species	Strain
Actinomycetota	Micrococcales	Micrococcaceae	*Micrococcus*	2	3
			Kocuria	1	1
	Mycobacteriales	Dietziaceae	*Dietzia*	1	2
		Corynebacteriaceae	*Corynebacterium*	1	1
Actinobacteria	Microbacteriales	Microbacteriaceae	*Microbacterium*	1	18
	Mycobacteriales	Nocardiaceae	*Rhodococcus*	2	2
	Micrococcales	Micrococcaceae	*Arthrobacter*	2	2
Pseudomonadota	Enterobacterales	Enterobacteriaceae	*Enterobacter*	3	7
			Klebsiella	1	9
			Escherichia	1	1
	Pseudomonadales	Pseudomonadaceae	*Pseudomonas*	2	3
Firmicutes	Bacillales	Bacillaceae	*Bacillus*	9	91

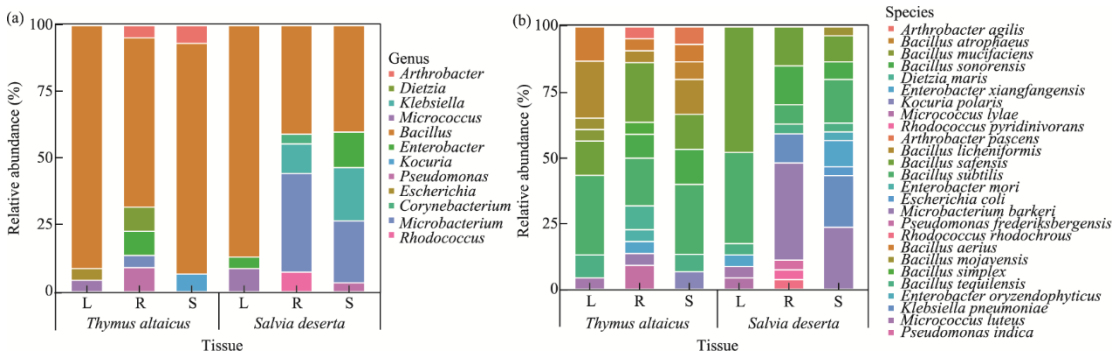

Fig. 1 Relative abundance of endophytic bacterial strains isolated from different tissues of *Thymus altaicus* and *Salvia deserta* at the genus level (a) and species level (b). L, leaf; R, root; S, stem.

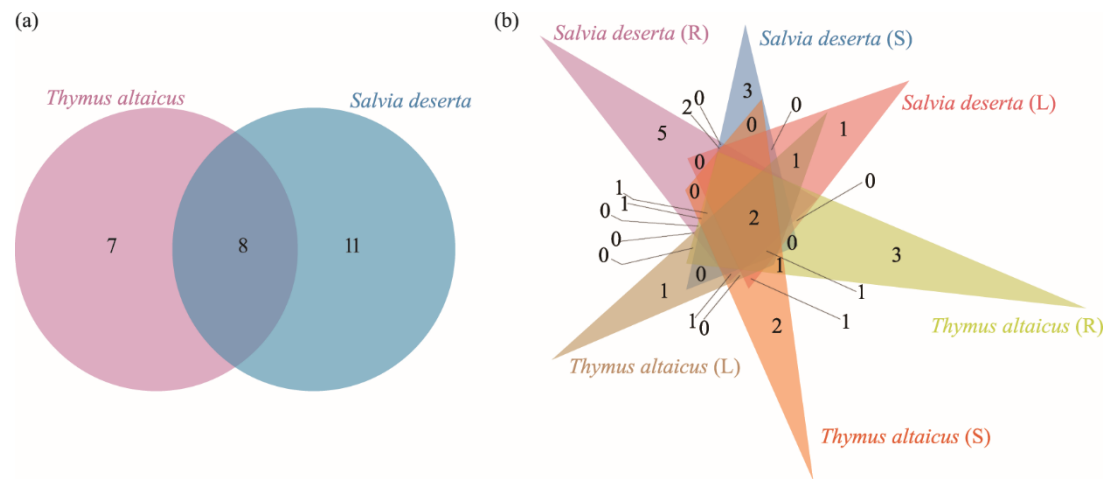

Fig. 2 Venn distribution of endophytic species in *Thymus altaicus* and *Salvia deserta*. (a), distribution between *Thymus altaicus* and *Salvia deserta*; (b), distribution among different tissues of *Thymus altaicus* and *Salvia deserta*.

2.1.3 Culture and screening media

In the present study, the compositions of the media utilized are displayed in Table 2. Medium 2 was employed for bacterial purification, while Medium 1 was applied in the assessment of anti-fungal activity through antagonistic assays. Additionally, Media 3–9 were utilized in the determination of plant growth-promoting properties.

2.2 Experimental methods

2.2.1 Determination of plant growth-promoting properties

In August 2022, the plant growth-promoting properties of 140 endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* were assessed at the State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences. The strains were inoculated in screening media (Table 2) and incubated at 30°C for 5–7 d to evaluate their enzyme-producing activities (including protease, cellulase, lipase, phosphate solubilization, siderophore, and chitinase) and nitrogen-fixing activity. The enzyme-producing activity was determined using Equation 1 as described by Gao et al. (2021):

$$E = \frac{D_1}{D_2}, \tag{1}$$

where E represents each enzyme-producing activity of the endophytic bacterial strain; D_1 is the diameter of the transparent circles formed by the enzyme-producing activity of the endophytic bacterial strain (mm); and D_2 is the diameter of the endophytic bacterial strain colony (mm). The criteria for assessing enzyme-producing activities can be found in Table 3.

Table 2 Composition of the media used in the current study

Medium no.	Medium name	Medium component (g/L)	Reference
1	PDA	Potato: 200.0 g/L; glucose: 20.0 g/L; agar: 15.0 g/L.	Liu et al. (2017)
2	ISP2	Glucose: 4.0 g/L; yeast extract: 4.0 g/L; malt extract: 10.0 g/L; agar: 15.0 g/L.	Liu et al. (2017)
3	Milk medium	D-mannitol: 10.0 g/L; yeast extract: 3.0 g/L; K_2HPO_4: 0.49 g/L; $MgSO_4·7H_2O$ 0.2 g/L; skim milk: 50.0 g/L; agar: 15.0 g/L.	Li et al. (2018)
4	CMC-Na medium	CMC-Na: 20.0 g/L; Na_2HPO_4: 2.5 g/L; KH_2PO_4: 1.5 g/L; peptone: 2.5 g/L; agar: 15.0 g/L.	Li et al. (2018)
5	Lipase medium	Peptone: 10.0 g/L; NaCl: 5.0 g/L; $CaCl_2$: 0.1 g/L; ferric citrate: 0.2 g/L; beef extract: 3.0 g/L; agar: 15.0 g/L.	Li et al. (2018)
6	Dephosphori-zation medium	Yeast extract: 0.5 g/L; glucose: 10.0 g/L; $(NH_4)_2SO_4$: 0.5 g/L; $MgSO_4·7H_2O$: 0.1 g/L; KCl: 0.2 g/L; NaCl: 0.2 g/L; $FeSO_4·7H_2O$: 2.0 mg/L; $MnSO_4·H_2O$: 2.0 mg/L; $Ca_3(PO_4)_2$: 5.0 g/L; bromophenol blue: 25.0 g/L; agar: 15.0 g/L.	Liu et al. (2017)
7	Chitinase medium	Chitin colloid: 4.5 g/L; anhydrous citric acid: 1.0 g/L; bromocresol purple: 150.0 mg/L; tween 20: 200.0 μL/L; $MgSO_4·7H_2O$: 0.3 g/L; $(NH_4)_2SO_4$: 3.0 g/L; KH_2PO_4: 2.0 g/L; agar: 15.0 g/L.	Agrawal and Kotasthane (2012)
8	CAS medium	CAS: 0.0605 g/L; $FeCl_3·6H_2O$ (10 mM HCL dissolved): 10.0 mL; HDTMA: 0.0728 g/L; K_2HPO_4: 0.3 g/L; NaCl: 0.5 g/L; PIPES: 30.4 g/L; NH_4Cl: 1.0 g/L; Mannitol: 2.0 g/L; $MgSO_4·7H_2O$: 0.493 g/L; $CaCl_2$: 0.011 g/L; $MnSO_4·H_2O$: 0.00117 g/L; H_3BO_3: 0.0014 g/L; $CuSO_4·5H_2O$: 0.04 mg/L; $ZnSO_4·7H_2O$: 0.0012 mg/L; $Na_2MoO_4·2H_2O$: 0.001 g/L; Casamino acids (10%; weight/volume): 30.0 mL; Glucose: 2.0 g/L; Agar: 15.0 g/L.	Liu et al. (2017)
9	Nitrogen fixation medium	D-mannitol: 10.0 g/L; K_2HPO_4: 0.2 g/L; $MgSO_4·7H_2O$: 0.2 g/L; NaCl: 0.2 g/L; $CaCO_3$: 5.0 g/L; $CaSO_4·2H_2O$: 0.2 g/L; Agar: 15.0 g/L.	Liu et al. (2017)

Note: PDA, Potato Dextrose Agar; ISP2, International Streptomyces Project-2 Medium; CMC, Carboxy Methyl Cellulose; CAS, Chrome Azurol Sulphonate; HDTMA, Hexadecy-trimethyl-ammonium Bromide; PIPES, Piperazine-1,4-bisethanesulfonic Acid.

Table 3 Criteria for determining different enzyme-producing activities of endophytic bacterial strains

Activity	Positive			Negative
	Strong	Moderate	Weak	
Protease-producing	$2.2 \le E < 2.8$	$1.6 \le E < 2.2$	$1.0 < E < 1.6$	$E \le 1.0$
Cellulase-producing	$4.9 \le E < 7.1$	$2.8 \le E < 4.9$	$1.0 < E < 2.8$	$E \le 1.0$
Lipase-producing	$3.1 \le E < 4.1$	$2.1 \le E < 3.1$	$1.0 < E < 2.1$	$E \le 1.0$
Phosphate solubilization	$2.0 \le E < 2.5$	$1.5 \le E < 2.0$	$1.0 < E < 1.5$	$E \le 1.0$
Siderophore-producing	$3.0 \le E < 4.0$	$2.0 \le E < 3.0$	$1.0 < E < 2.0$	$E \le 1.0$
Chitinase-producing		$E > 1.0$		$E \le 1.0$
Nitrogen-fixing		$E > 1.0$		$E \le 1.0$

Note: E, enzyme-producing activity of endophytic bacterial strain.

2.2.2 Antagonistic assays of anti-fungal activity

In this study, endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* exhibiting anti-fungal activity against pathogenic fungi were identified using the plate confrontation method (Liu et al., 2017). This investigation was conducted at the State Key Laboratory of Desert and Oasis Ecology, Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences in August 2022. The anti-fungal activity of these endophytic bacterial strains against pathogenic fungi was assessed using Equation 2:

$$I = \frac{D_0 - D_i}{D_0} \times 100\%, \quad (2)$$

where I represents the inhibition rate (%); D_0 denotes the diameter of fungal colony on the control Potato Dextrose Agar (PDA) base plate (mm); and D_i signifies the diameter of fungal colony on

the experimental PDA base plate (mm).

From the initial screening results, strains exhibiting inhibition rates of <30.0% against *Fulvia fulva*, *Alternaria solani*, *Fusarium oxysporum*, and *Valsa mali* showed negative anti-fungal activity. Strains with inhibition rates higher than 30.0% showed positive anti-fungal activity, which were selected for further analysis. Strains with inhibition rates of 30.0%–45.0% were classified as weak antagonism, 45.0%–60.0% as moderate antagonism, and ≥60.0% as strong antagonism.

2.3 Data analysis

The experiments were conducted in triplicate, and the analyses were replicated to confirm the reliability of the outcomes. Initial data processing was performed using Microsoft Excel 2013, while statistical analysis was carried out with SPSS 22.0. Additionally, R 4.2.1 and Origin 20.0 were employed for the creation of graphical representations.

3 Results

3.1 Plant growth-promoting properties

In this investigation, the 80 endophytic bacterial strains isolated from *Thymus altaicus* exhibited various enzyme-producing activities: 37 strains with protease-producing activity, 53 with cellulase-producing activity, 38 with lipase-producing activity, 16 with phosphate solubilization activity, 24 with chitinase-producing activity, 43 with siderophore-producing activity, and 67 with nitrogen-fixing activity (Table 4). Among these, 1, 14, 2, 3, and 7 strains exhibited strong activities in protease-producing, cellulase-producing, lipase-producing, phosphate solubilization, and siderophore-producing, respectively. In contrast, among the 60 endophytic bacterial strains isolated from *Salvia deserta*, 35, 50, 34, 6, 8, 38, and 45 strains demonstrated protease-producing activity, cellulase-producing activity, lipase-producing activity, phosphate solubilization activity, chitinase-producing activity, siderophore-producing activity, and nitrogen-fixing activity, respectively (Table 5). Of these, 3, 6, 2, 0, and 7 strains displayed strong activities in protease-producing, cellulase-producing, lipase-producing, phosphate solubilization, and siderophore-producing, respectively.

Comparatively, the 60 endophytic bacterial strains isolated from *Salvia deserta* exhibited stronger protease-producing activity, cellulase-producing activity, lipase-producing activity, and siderophore-producing activity than those isolated from *Thymus altaicus*. However, the endophytic bacterial strains of *Thymus altaicus* demonstrated stronger chitinase-producing activity, phosphate solubilization activity, and nitrogen-fixing activity than those of *Salvia*

Table 4 Number and percentage of endophytic bacterial strains isolated from *Thymus altaicus* with different enzyme-producing activities reflecting plant growth-promoting properties

Activity	Positive								Negative	
	Strong		Moderate		Weak		Total		Number	PERC (%)
	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)		
Protease-producing	1	2.7	8	21.6	28	75.7	37	46.3	43	53.7
Cellulase-producing	14	26.4	22	41.5	17	32.1	53	66.3	27	33.7
Lipase-producing	2	5.3	10	26.3	26	68.4	38	47.5	42	52.5
Phosphate solubilization	3	18.8	6	37.5	7	43.7	16	20.0	64	80.0
Chitinase-producing	-	-	-	-	-	-	24	30.0	56	70.0
Siderophore-producing	7	16.3	17	39.5	19	44.2	43	53.8	37	46.2
Nitrogen-fixing	-	-	-	-	-	-	67	83.8	13	16.2

Note: PERC, percentage. "-" means no data. The percentage in the "Strong", "Moderate", and "Weak" columns is the rate of the number in each column to the number in the "Total" column. The percentage in the "Total" column is the rate of the number of strains with positive activity to the number of strains with positive and negative activities.

Table 5 Number and percentage of endophytic bacterial strains isolated from *Salvia deserta* with different enzyme-producing activities reflecting plant growth-promoting properties

Activity	Positive								Negative	
	Strong		Moderate		Weak		Total		Number	PERC (%)
	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)		
Protease-producing	3	8.6	2	5.7	30	85.7	35	58.3	25	41.7
Cellulase-producing	6	12.0	33	66.0	11	22.0	50	83.3	10	16.7
Lipase-producing	2	5.9	8	23.5	24	70.6	34	56.7	26	43.3
Phosphate solubilization	0	0.0	1	16.7	5	83.3	6	10.0	54	90.0
Chitinase-producing	-	-	-	-	-	-	8	13.3	52	86.7
Siderophore-producing	7	18.4	14	36.8	17	44.8	38	63.3	22	36.7
Nitrogen-fixing	-	-	-	-	-	-	45	75.0	15	25.0

Note: "-" means no data.

deserta. Consequently, our findings indicate that these bacterial strains possess the potential to improve plant growth.

3.2 Anti-fungal activity

Endophytic bacterial strains exhibiting inhibition rates above 30.0% were identified as inhibitors. A total of 104 strains demonstrated anti-fungal activity, with 62, 65, 67, and 72 strains inhibiting *Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*, respectively (Tables 6 and 7). These strains belonged to genera such as *Bacillus* (80 strains), *Microbacterium* (6 strains), *Enterobacter* (5 strains), *Klebsiella* (4 strains), *Micrococcus* (2 strains), *Pseudomonas* (1 strain), *Corynebacterium* (1 strain), *Arthrobacter* (1 strain), *Rhodococcus* (1 strain), *Kocuria* (1 strain), *Escherichia* (1 strain), and *Dietzia* (1 strain).

Table 6 Number and percentage of endophytic bacterial strains isolated from *Thymus altaicus* showing anti-fungal activity against the four pathogenic fungi (*Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*)

Pathogenic fungi	Positive								Negative	
	Strong		Moderate		Weak		Total		Number	PERC (%)
	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)		
Fusarium oxysporum	17	50.0	13	38.2	4	11.8	34	42.5	46	57.5
Fulvia fulva	21	51.2	12	29.3	8	19.5	41	51.3	39	48.7
Alternaria solani	21	52.5	17	42.5	2	5.0	40	50.0	40	50.0
Valsa mali	11	26.2	21	50.0	10	23.8	42	52.5	38	47.5

Table 7 Number and percentage of endophytic bacterial strains isolated from *Salvia deserta* showing anti-fungal activity against the four pathogenic fungi (*Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*)

Pathogenic fungi	Positive								Negative	
	Strong		Moderate		Weak		Total			
	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)	Number	PERC (%)
Fusarium oxysporum	14	50.0	14	50.0	0	0.0	28	46.7	32	53.3
Fulvia fulva	10	41.7	9	37.5	5	20.8	24	40.0	36	60.0
Alternaria solani	17	63.0	9	33.3	1	3.7	27	45.0	33	55.0
Valsa mali	3	10.0	13	43.3	14	46.7	30	50.0	30	50.0

For *Thymus altaicus*, 34, 41, 40, and 42 endophytic bacterial strains were antagonistic against *Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*, respectively (Table 6). Among these, 17, 21, 21, and 11 strains exhibited strong antagonism against *Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*, respectively. For *Salvia deserta*, 28, 24, 27, and 30 endophytic bacterial strains displayed anti-fungal activity against *Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*, respectively (Table 7). Of these, 14, 10, 17, and 3 strains exhibited strong antagonism against *Fusarium oxysporum*, *Fulvia fulva*, *Alternaria solani*, and *Valsa mali*, respectively.

In this study, *Bacillus* sp. TS011 demonstrated the most potent antagonism against *Fulva fulva*, with an inhibition rate of 71.3% (Table S1); *Bacillus* sp. TLB015 exhibited the strongest antagonism against *Alternaria solani*, with an inhibition rate of 77.0%; *Bacillus* sp. SL007 displayed the most robust antagonism against *Fusarium oxysporum*, with an inhibition rate of 71.0%; and *Bacillus* sp. TRB020 showed intense antagonism against *Valsa mali*, with an inhibition rate of 71.7%. Additionally, we observed that the number of endophytic bacterial strains with anti-fungal activity against *Fusarium oxysporum* isolated from *Salvia deserta* exceeded the number of endophytic bacterial strains isolated from *Thymus altaicus* against *Fusarium oxysporum*. However, endophytic bacterial strains isolated from *Thymus altaicus* exhibited greater advantages in inhibiting pathogenic fungi.

Overall, 39 endophytic bacterial strains displayed anti-fungal activity against the four pathogenic fungi, distributed among *Bacillus* (36 strains), *Klebsiella* (1 strain), *Arthrobacter* (1 strain), and *Enterobacter* (1 strain), accounting for 92.3%, 2.6%, 2.6%, and 2.6% of the 39 endophytic bacterial strains, respectively. Most of these strains demonstrated a strong antagonism, suggesting that these 39 endophytic bacterial strains could effectively inhibit plant fungi. Furthermore, 22 of the 80 tested endophytic bacterial strains (27.5%) isolated from *Thymus altaicus* displayed a broad anti-fungal spectrum, such as *Bacillus* sp. TS003 and *Bacillus* sp. TSB7, both exhibiting strong antagonism against the four pathogenic fungi (Table S1). In contrast, 17 of the 60 tested endophytic bacterial strains (28.3%) isolated from *Salvia deserta* showed a broad anti-fungal spectrum. These results indicated that the number of endophytic bacterial strains with a broad anti-fungal spectrum in *Salvia deserta* exceeded that in *Thymus altaicus*, suggesting that the strains isolated from *Salvia deserta* could serve as more promising biocontrol agents against plant pathogens, compared to those isolated from *Thymus altaicus*.

4 Discussion

Endophytes establish various symbiotic relationships with their host plants, promoting plant growth, enhancing adaptability, and increasing resistance to biotic and abiotic stresses (Kandel et al., 2017). In this study, the growth-promoting properties and anti-fungal activity of endophytic bacterial strains isolated from two medicinal plant species, *Thymus altaicus* and *Salvia deserta*, were investigated. The results demonstrated that endophytic bacterial strains isolated from both plant species exhibited growth-promoting properties. Previous research has shown that microbial enzymes, such as lipase, protease, cellulase, and chitinase, possess significant biocontrol potential and can protect plants from various pathogens (Mishra et al., 2020). El-Shatoury et al. (2009) discovered that endophytic bacterial strains isolated from *Achillea fragrantissima* produced siderophores and chitinase, while also exhibiting a notable inhibitory effect on tested pathogenic fungi.

Endophytic bacterial genus *Bacillus* has been found to promote plant growth through nitrogen fixation, phosphorus solubilization, phytohormone production, and ferri carrier production (Khan et al., 2022). *Bacillus* sp. TR005 exhibited strong siderophore-producing activity, cellulase-producing activity, and extensive inhibition against the four pathogenic fungi, making it a valuable biocontrol agent (Rungin et al., 2012). In this study, 20.0% and 10.0% of endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* displayed phosphate solubilization activity, respectively, while 83.8% and 75.0% of endophytic bacterial strains isolated from *Thymus*

altaicus and *Salvia deserta* exhibited nitrogen-fixing activity, respectively. Joshi et al. (2019) reported that *Rhodococcus qingshengii* S10107, a strain with robust nitrogen-fixing activity, promoted the growth and development of chickpea. In this study, *Rhodococcus* sp. TR013 demonstrated strong nitrogen-fixing activity and could be further explored as a nitrogen source for plant growth. Kaur et al. (2011) found that *Microbacterium paraoxydans* W1-PSB2, a strain isolated from wheat roots, displayed potent phosphate solubilization activity. Kumar et al. (2017) showed that co-inoculation of *Serratia marcescens*, *Microbacterium arborescens*, and *Enterobacter* sp. could increase plant height, straw yield, grain yield, and test weight of wheat in both pot and field trials. The endophytic bacterial strain *Microbacterium* sp. TSB5 was found to be highly effective in phospholysis, suggesting that *Microbacterium* strains could be further developed as potential bacterial agents with phospholysis effects for field and environmental applications.

This study screened 104 endophytic bacterial strains with anti-fungal activity, of which strains of *Bacillus* genus accounted for 76.9% of the total, indicating the potential of this genus for controlling plant pathogens. For instance, Xu et al. (2020) discovered that *Bacillus* sp. WB inhibited the growth of *Fusarium oxysporum* f. sp. *niveum*, altered the microbial community structure of watermelon, and promoted its growth and development. Gao et al. (2017) found that *Bacillus velezensis* ZSY-1, a strain producing unique volatile compounds, was effective against pathogenic fungi such as *Alternaria solani*, *Botrytis cinerea*, *Valsa mali*, *Monilinia fructicola*, *Fusarium oxysporum* f. sp. *Capsicum*, and *Colletotrichum lindemuthianum*. Isolating the endophytic bacteria of *Bacillus* genus is significant, as the strains can produce secondary metabolites used in various biotechnologies, including food, pharmaceutical, environmental, and industrial applications (Kumar et al., 2014). The pathogen inhibition mechanism of plant endophytic bacteria with inhibitory effects identified in this study requires further investigation. Additionally, we found that *Enterobacter* sp. TSB031 exhibited strong antagonism, corroborating the findings of Kavroulakis et al. (2010). *Enterobacter* sp. TSB031 also demonstrated anti-fungal activity against *Fulvia fulva*, *Alternaria solani*, *Fusarium oxysporum*, and *Valsa mali*, suggesting its potential for biocontrol development.

Endophytic bacterial strains isolated from medicinal plants with anti-fungal activity show promise for the biocontrol of plant diseases (Cardoso et al., 2020). Metabolites produced by endophytes can enhance host plant resistance to diseases and increase the synthesis of substances with antipest, antipathogen, antiviral, and antitumor activities. This study indicates that endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* displayed potent antagonism against various pathogenic fungi, making them promising candidates for plant growth promotion and pathogen inhibition in future research.

5 Conclusions

In this investigation, we examined the plant growth-promoting properties and anti-fungal activity of endophytic bacterial strains isolated from two medicinal plant species, *Thymus altaicus* and *Salvia deserta*. Our findings revealed that all endophytic bacterial strains isolated from both *Thymus altaicus* and *Salvia deserta* exhibited growth-promoting properties, with a total of 104 strains demonstrating anti-fungal activity against the four pathogenic fungi: *Fulvia fulva*, *Alternaria solani*, *Fusarium oxysporum*, *and Valsa mali. Bacillus* sp. TR005 strain not only displayed robust siderophore-producing activity but also exhibited a broad spectrum of antagonism against the four pathogenic fungi. Consequently, *Bacillus* sp. TR005 strain possesses significant potential for application in plant disease management. These findings indicate that medicinal plants can serve as a valuable resource for enhancing plant growth and safeguarding plants against diseases. As such, endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* hold considerable ecological importance in agricultural production. Furthermore, additional research is required to identify strains with in vitro plant growth-promoting properties and anti-fungal activity for use in plant growth chamber experiments.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was financially supported by the Third Xinjiang Comprehensive Scientific Expedition (2022xjkk-020605) and the Xinjiang Uygur Autonomous Region Regional Coordinated Innovation Project (Shanghai Cooperation Organization Science and Technology Partnership Program) (2020E01047). This study was also supported by the Introduction Project of High-level Talents in Xinjiang Uygur Autonomous Region, China. We are grateful to Mr. ZHANG Zheng, Mr. CUI Lei, and Mr. XU Qingyu from the Xinjiang Institute of Ecology and Geology, Chinese Academy of Sciences, as well as Mr. ZHANG Hailong and Mr. ZHU Jin from the College of Life Science and Technology, Xinjiang University, for their valuable assistance in the phenotypic characterization and identification of the endophytic bacterial strains. Special appreciation to the anonymous reviewers for their insightful and constructive comments on the manuscript.

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Appendix

Table S1 Inhibition rates of tested endophytic bacterial strains isolated from *Thymus altaicus* and *Salvia deserta* against the four pathogenic fungi (*Fulvia fulva*, *Alternaria solani*, *Fusarium oxysporum*, and *Valsa mali*)

Strain	Inhibition rate (%)			
	Fulvia fulva	*Alternaria solani*	*Fusarium oxysporum*	*Valsa mali*
Bacillus sp. TL001	54.6	53.2	65.5	68.0
Micrococcus sp. TL002	54.7	67.5	46.9	-
Enterobacter sp. TL003	-	65.0	-	-
Bacillus sp. TL004	-	50.7	-	63.3
Bacillus sp. TL006	65.0	73.0	70.0	68.7
Microbacterium sp. TR001	-	-	-	-
Bacillus sp. TR002	-	-	-	45.6
Microbacterium sp. TR003	-	-	-	-
Microbacterium sp. TR004	-	-	-	-
Bacillus sp. TR005	67.0	65.4	58.8	50.8
Rhodococcus sp. TR007	-	56.0	-	-
Microbacterium sp. TR009	-	-	-	-
Rhodococcus sp. TR013	-	-	-	-
Microbacterium sp. TR015	-	-	-	32.7
Microbacterium sp. TR016	-	-	-	38.2
Bacillus sp. TS001	69.3	58.5	57.0	48.1
Bacillus sp. TS002	66.2	55.7	60.1	56.2
Bacillus sp. TS003	67.5	73.9	63.0	61.4
Enterobacter sp. TS004	61.0	65.0	60.3	-
Microbacterium sp. TS005	-	-	-	-
Bacillus sp. TS006	70.3	59.0	53.3	68.7
Microbacterium sp. TS009	-	-	-	-
Bacillus sp. TS011	71.3	48.9	48.1	65.0
Microbacterium sp. TS012	-	-	-	-
Microbacterium sp. TS013	-	-	-	-
Bacillus sp. TS014	-	-	-	61.2
Microbacterium sp. TS015	-	-	-	-
Bacillus sp. TS016	-	-	-	54.6
Bacillus sp. TS018	-	-	-	52.1
Klebsiella sp. TS B3	-	51.5	40.6	-
Microbacterium sp. TS B5	-	-	-	-
Klebsiella sp. TS B6	-	-	-	-
Bacillus sp. TS B7	65.2	67.7	60.9	64.9
Enterobacter sp. TSB018	-	-	-	-
Klebsiella sp. TSB019	-	-	-	-

Strain	Inhibition rate (%)			
	Fulvia fulva	*Alternaria solani*	*Fusarium oxysporum*	*Valsa mali*
Klebsiella sp. TSB020	-	-	-	-
Klebsiella sp. TSB022	-	-	44.3	-
Enterobacter sp. TSB023	-	-	-	31.9
Escherichia sp. TSB024	63.0	-	-	-
Bacillus sp. TSB025	56.3	60.1	66.8	-
Enterobacter sp. TSB031	43.0	51.0	68.0	59.5
Klebsiella sp. TSB034	-	-	-	-
Bacillus sp. TSB035	69.2	70.0	65.2	64.3
Bacillus sp. TSB036	59.0	70.0	61.9	65.7
Microbacterium sp. TSB037	53.1	-	-	-
Bacillus sp. TR B1	69.8	74.2	66.1	51.2
Bacillus sp. TR B2	65.2	67.1	58.2	35.8
Bacillus sp. TR B3	68.3	64.0	62.2	56.2
Klebsiella sp. TR B6	-	-	-	-
Klebsiella sp. TR B7	40.5	48.2	-	-
Bacillus sp. TR B8	-	-	-	45.6
Microbacterium sp. TR B10	51.1	-	-	48.8
Microbacterium sp. TR B11	-	-	-	48.8
Microbacterium sp. TR B14	44.4	44.5	41.2	-
Bacillus sp. TRB016	51.7	-	-	45.2
Bacillus sp. TRB020	62.3	58.0	55.1	71.7
Bacillus sp. TRB021	70.0	62.9	65.3	53.7
Pseudomonas sp. TRB022	-	45.7	31.3	-
Klebsiella sp. TRB023	57.2	53.4	55.9	53.4
Microbacterium sp. TRB025	-	-	-	-
Bacillus sp. TRB027	66.8	67.9	47.5	-
Bacillus sp. TRB028	40.2	47.1	-	-
Micrococcus sp. TL B1	55.3	46.5	-	-
Bacillus sp. TL B2	56.5	53.8	57.6	47.9
Bacillus sp. TL B3	61.8	62.8	65.7	59.8
Bacillus sp. TL B4	43.8	-	47.1	-
Bacillus sp. TL B6	-	-	-	37.9
Bacillus sp. TL B7	-	-	-	43.5
Bacillus sp. TL B9	-	-	-	50.4
Bacillus sp. TL B10	-	-	-	31.9
Bacillus sp. TL B11	-	-	-	-
Bacillus sp. TL B13	-	-	-	45.2
Bacillus sp. TL B14	41.3	-	-	39.0

Strain	Inhibition rate (%)			
	Fulvia fulva	*Alternaria solani*	*Fusarium oxysporum*	*Valsa mali*
Bacillus sp. TL B15	70.4	71.6	62.2	-
Bacillus sp. TL B16	66.5	71.2	59.2	41.7
Bacillus sp. TLB011	39.3	42.9	-	40.5
Bacillus sp. TLB013	41.1	46.8	-	-
Bacillus sp. TLB014	68.3	74.8	62.6	-
Bacillus sp. TLB015	55.2	77.0	62.4	52.5
Bacillus sp. TLB017	52.5	69.8	57.6	52.9
Bacillus sp. SR001	-	-	-	41.3
Bacillus sp. SR002	-	-	-	-
Bacillus sp. SR003	-	-	-	40.3
Bacillus sp. SR004	-	-	-	41.0
Bacillus sp. SR006	55.3	53.4	60.3	38.2
Arthrobacter sp. SR009	-	-	-	-
Pseudomonas sp. SR011	-	-	-	-
Bacillus sp. SR012	59.4	69.6	61.9	-
Microbacterium sp. SR014	-	-	-	-
Dietzia sp. SR015	-	-	-	-
Enterobacter sp. SR017	-	-	-	-
Bacillus sp. SR020	44.8	59.1	57.6	-
Pseudomonas sp. SR023	-	-	-	-
Bacillus sp. SS003	45.2	63.6	58.3	56.9
Bacillus sp. SS005	61.6	65.2	59.2	-
Arthrobacter sp. SS006	61.7	66	58.5	58.5
Bacillus sp. SS007	-	-	-	-
Kocuria sp. SS008	-	-	-	56.9
Bacillus sp. SL001	62.5	57.3	62.0	46.6
Bacillus sp. SL001a	56.4	54.4	62.6	43.6
Bacillus sp. SL001b	61.9	58.1	60.8	42.5
Bacillus sp. SL002	51.3	-	-	-
Bacillus sp. SL003	-	-	-	-
Bacillus sp. SL004	-	39.0	-	-
Bacillus sp. SL005	-	-	-	36.3
Bacillus sp. SL006	64.4	70.0	61.2	66.8
Bacillus sp. SL007	67.3	70.3	71.0	67.2
Bacillus sp. SL008	56.5	48.1	58.8	63.3
Bacillus sp. SL009	62.9	63.0	53.0	51.7
Bacillus sp. SL011	-	-	-	47.5
Micrococcus sp. SL012	-	-	-	-

Strain	Inhibition rate (%)			
	Fulvia fulva	*Alternaria solani*	*Fusarium oxysporum*	*Valsa mali*
Bacillus sp. SR B1	-	-	-	45.9
Dietzia sp. SR B2	-	51.5	-	-
Bacillus sp. SRB023	-	-	-	36.7
Bacillus sp. SRB025	-	-	-	40.6
Bacillus sp. SRB026	55.3	48.4	66.9	45.2
Enterobacter sp. SRB027	-	-	55.5	-
Bacillus sp. SRB028	-	-	-	-
Bacillus sp. SRB032	-	-	-	-
Bacillus sp. SRB034	-	74.8	63.2	-
Bacillus sp. SS B1	-	-	-	-
Bacillus sp. SS B3	30.7	-	-	41.0
Bacillus sp. SS B4	30.7	70.9	63.0	51.6
Bacillus sp. SSB012	35.3	66.1	58.1	54.8
Bacillus sp. SSB013	-	61.6	67.2	-
Bacillus sp. SSB014	-	-	-	-
Bacillus sp. SSB015	54.0	70.3	64.1	57.1
Bacillus sp. SSB016	55.3	62.2	53.0	44.0
Bacillus sp. SSB019	63.1	68.6	64.3	49.0
Bacillus sp. SSB020	-	47.6	53.6	32.0
Corynebacterium sp. SL B1	63.1	66.1	53.1	-
Bacillus sp. SL B2	66.2	66.4	63.8	47.0
Bacillus sp. SL B6	44.1	-	-	37.8
Bacillus sp. SLB010	-	-	59.2	-
Bacillus sp. SLB011	-	-	-	-
Bacillus sp. SLB013	-	-	58.5	-
Bacillus sp. SLB015	-	68.6	50.7	-
Bacillus sp. SLB016	-	-	-	-
Bacillus sp. SLB017	-	-	-	-
Bacillus sp. SLB018	-	-	-	33.6

Note: "-" means the tested strain is negative for inhibiting the corresponding pathogenic fungi.